COMMENTS UPON THE ORIGIN OF THE HERPETOFAUNA OF FLORIDA

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The fauna of Florida, with its relatively large number of endemics, has been a perennial source of stimulation to zoogeographers. Because of this it would seem that the origin of the Floridian fauna would long ago have been adequately discussed. It seems to me that there are two basic reasons why this is not so. One is the continuing growth in our knowledge of the geology of Florida and the other is the accumulation of new fossil material from Florida. Dr. Robert O. Vernon (1951) gives, for example, a somewhat different interpretation of Cenozoic land masses in Florida than does Cooke (1945). Also, recent studies in Floridian paleontology (see Tihen, 1951; Goin and Auffenberg, 1955; Auffenberg, 1956a, 1958) throw additional light on the early herpetofauna of Florida. Since we now have this additional knowledge of the Cenozoic amphibians and reptiles and these new interpretations of the land masses, it might be profitable to re-examine ideas concerning the zoogeographic relationships of the present Florida herpetofauna.

An examination of the recent amphibians and reptiles of Florida shows that on the basis of geographic affinities they can be divided into five more or less distinctive groups. These are:

Tropicopolitan
Antillean
Northeastern
Southwestern and Mexican
Southeastern and Floridian

These will be discussed in order.

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[1] This paper is an outgrowth of one presented several years ago in a symposium on the origin of the fauna and flora of Florida at a meeting of the Florida Academy of Science. At the time I was revising it for publication my friend, Wilfred T. Neill, of Ross Allen's Reptile Institute, independently began work on his study "Historical Biography of Present-day Florida." His paper has since been published as a Bulletin of the Florida State Museum, Vol. 2, no. 7, pp. 175-220, 1957. Since he emphasized the ecological, while I have emphasized the geological, aspects, however, the two papers tend to supplement one another.

I wish to acknowledge my indebtedness to my colleague, Dr. Walter Auffenberg, for the help he has given me in the preparation of this paper.

Tropicopolitan

This group contains no amphibians and only seven genera of reptiles. They are:

Salamanders 0
Frogs 0
Crocodilians 1
Crocodylus
Turtles 5
Chelonia
Eretmochelys
Caretta
Lepidochelys
Dermochelys
Lizards 1
Hemidactylus
Snakes 0

As can be seen, this group comprises primarily the large marine turtles and the marine crocodile. The genus *Hemidactylus* is now wide-spread throughout the tropics of both the Old and New World. It extends from northwestern India westward into eastern Africa, south at least to Kenya, along the coast of the Red Sea and the coastal islands of the Mediterranean; in the New World it is found in the West Indies and in Key West and the Miami region of Florida. There is nothing about this group that deserves special comment.

Antillean

This small group contains forms that have reached Florida from the Antilles. It includes one frog and four lizards.

Salamanders 0
Frogs 1
Eleutherodactylus
Crocodilians 0
Turtles 0
Lizards 4
Gonatodes
Sphaerodactylus
Anolis
Leiocephalus
Snakes 0

The genera in the above list are unquestionably of Antillean derivation. *Anolis* was present in the Pleistocene of Florida. *Eleutherodactylus, Gonatodes, Sphaerodactylus* and *Leiocephalus,* on the other hand, probably arrived here in post-Columbian times. Like the first group, this one does not really require much comment.

Northeastern

As might be expected, a large portion of the genera of amphibians and reptiles that now occupy Florida are southern extensions of

populations occupying the eastern United States. The following list includes those forms that seem to me simple derivatives of northeastern genera.

Salamanders 7
- *Necturus*
- *Diemictylus*
- *Ambystoma*
- *Plethodon*
- *Eurycea*
- *Pseudotriton*
- *Desmognathus*

Frogs 3
- *Acris*
- *Pseudacris*
- *Rana*

Crocodilians 0

Turtles 6
- *Sternotherus*
- *Chelydra*
- *Chrysemys*
- *Malaclemmys*
- *Graptemys*
- *Trionyx*

Lizards 0

Snakes 7
- *Carphophis*
- *Opheodrys*
- *Elaphe*
- *Natrix*
- *Storeria*
- *Haldea*
- *Sistrurus*

Examination of this list shows that the genera are basically of two sorts: those like *Necturus, Pseudotriton* and *Acris* that are found only in eastern United States; and those like *Rana, Trionyx* (*sensu latu*), *Elaphe* and *Natrix* that are present in both the Old and the New World but in the New World are restricted largely to the eastern United States. There are two notable things about the above list. One is the predominance of salamanders, which seems to bear out the contention that the eastern United States has been a center of late evolution for this group. The other is the abundance of small natricine snakes which supports the conclusion of Dunn (1931) that the natricines belong to the group which he calls the "Old Northern".

Southwestern and Mexican

This group includes those genera that presumably came in from the west to occupy Florida. The list is as follows:

Salamanders 0

Frogs 4
- *Scaphiopus*
- *Bufo*
- *Hyla*
- *Microhyla*

Crocodilians 0

Turtles 4
- *Kinosternon*
- *Terrapene*

Pseudemys
Gopherus
Lizards 6
Sceloporus
Ophisaurus
Phrynosoma
Cnemidophorus
Lygosoma
Eumeces
Snakes 12
Diadophis
Heterodon
Coluber
Drymarchon
Pituophis
Rhadinaea
Lampropeltis
Thamnophis
Tantilla
Micrurus
Agkistrodon
Crotalus

Florida has a relatively small lizard fauna, but such lizards as are present are basically either forms from the West or introduced Antillean and Tropicopolitan forms plus a few arenicolus genera to be discussed later. Among the snakes it might be noted also that the Florida snake population that has apparently been derived from western stock contains a large percentage of big snakes, such as *Coluber, Drymarchon, Pituophis, Lampropeltis, Agkistrodon* and *Crotalus,* in contrast to the small snakes of the previous list, *Carphophis, Storeria, Haldea, Sistrurus.*

Southeastern or Floridian

Salamanders 4
Amphiuma
Manculus
Siren
Pseudobranchus
Frogs 0
Crocodilians 1
Alligator
Turtles 2
Macroclemmys
Dierochelys
Lizards 2
Neoseps
Rhineura
Snakes 6
Abastor
Farancia
Stilosoma
Cemophora
Seminatrix
Liodytes

Except for the addition of forms more widely distributed in the Southeast, such as *Amphiuma, Siren, Deirochelys, Abastor* and *Farancia,* this is not too different from the list of endemic genera given by Carr (1940). It is this list that contains the forms that we now want to examine in the light of modern geologic interpretations and paleontological evidence.

It seems likely that there are really two sorts of populations contained in the above list, first, relicts of what were once more wide-spread stocks and second, true endemics that have originated and persisted here. Let us look at the evidence for each.

We know that *Alligator* is nothing but an example of a relict distribution of a once wide-spread population since the fossil record indicates an earlier more extensive distribution. Indeed it is still in existence today in southeastern Asia as well as in the southeastern United States.

Another example of a remnant of a once more widely distributed form is the Alligator Snapping Turtle, *Macroclemmys,* which now occurs only on the lower coastal plain from the Mississippi River to the Okefinokee Swamp although it is known from the Miocene and Pliocene of Nebraska.

At the present time the family Sirenidae comprises two genera. *Siren* has two species, *lacertina* of the Southeast and the wide-ranging *intermedia* which extends as far as extreme northeastern Mexico. *Pseudobranchus,* with its several geographic races, is confined to the lower southeastern states, from about Charleston, South Carolina, south and west through peninsular Florida to just beyond the Apalachicola River.

At the time Carr (1940) prepared his list, the Sirenidae were unknown as fossils except for a few scattered Pleistocene records of *lacertina* from Florida. This is no longer so. Today the earliest record of any sirenid is from the Early Cretaceous Trinity sands of Montague County, Texas. From these beds were taken three vertebrae, two of them rather fragmental, which are assigned to an undescribed genus rather than to the modern genus *Siren.* The material is too scanty to yield much information about evolutionary lines, but it does, definitely, indicate the antiquity of the family and assures us that Sirenidae were present in the United States in the Lower Cretaceous. The next sirenid record is from the Upper Cretaceous of Wyoming where we have another undescribed genus. This is a much more "Siren" looking animal, but it too is assigned to a different genus. It does, however, indicate that the family was present in former times in regions where it does not occur today. We find true *Siren* in the Eocene of Wyoming, indicating that the genus *Siren* has existed throughout most of the Cenozoic and that it was earlier distributed in regions where it is not found at the present time.

None of these records, however, contributes to our knowledge of the zoogeography of Florida other than to indicate that the genus *Siren* was in existence well before there was a land mass in Florida to be occupied by it. Our first Floridian record is of *Siren hesterna* from the Lower Miocene of the Raeford Thomas farm in Gilchrist County. This Miocene record, of course, indicates only that there was a land mass with fresh water in Florida during the Lower Miocene and that *Siren* had been able to move in to occupy it. In the Alachua formation of the Pliocene we find the genus *Siren* still present and a recognizable, although as yet somewhat poorly differentiated, *Pseudobranchus,* so that for the first time we have two contemporary genera of Sirenidae at the same locality. Both genera were still present in the Pleistocene of Florida and are here today as well differentiated genera. The paleontological record thus indicates that the genus *Pseudobranchus* came into existence sometime before middle Pliocene times, probably directly from the genus *Siren,* and that the two have continued to live side by side and to differentiate. This is the sort of evidence that herpetologists have been looking for.

None of the herpetologists of my acquaintance has been willing to admit that such genera as *Neoseps, Rhineura, Stilosoma* and *Pseudobranchus* have arisen entirely in post-Pliocene times. Yet, until recently, geologists would not admit continuous land in peninsular Florida from the Pliocene to the present, and there was no paleontological evidence to the contrary. Now, however, this geologic interpretation has been abandoned, for Cooke (1945) has shown persistent, albeit small, islands in his latest map, and Vernon (1951) admits land since the Miocene. In further discussion of this problem, Dr. Vernon wrote me:

> "However, the area of Florida that extends from the Chattahoochee River to slightly east of the Suwannee River is a broad, flat plain, that I interpret as being a Miocene plain surface that is underlain by Middle-Miocene deposits. These deposits, in part, lie directly upon the Suwannee limestone of Oligocene age and no Tampa is present. This delta plain was an area that can be compared to the Mississippi Delta today, and it supported a large and diverse plains dwelling vertebrate animal group. The delta was developed upon a land surface that had existed through the Tampa time, and it was built throughout the Miocene. It has not been subsequently recovered by younger marine deposits."

With this interpretation that a relatively large land mass has been in continuous existence in Florida from the Middle Miocene to the present, and the knowledge that the genus *Pseudobranchus* is not a Post-Pliocene form, but rather arose sometime earlier, probably between the Lower Miocene and the Lower Pliocene, the picture is now entirely changed.

The paleontological data and the geologic interpretations thus would seem to indicate beyond a reasonable doubt that the genus *Siren* has been in Florida since the Lower Miocene, that at least some land mass has been permanent in Florida since those times; that on this land mass the genus *Siren* gave rise to the genus *Pseudobranchus;* and that since it arose *Pseudobranchus* has spread only slightly from its center of origin, up to South Carolina and west to beyond the Apalachicola River.

Although fossil evidence is lacking, I strongly suspect that other southeastern genera, such as *Manculus* and *Neoseps,* have had histories similar to that of *Pseudobranchus.* On the other hand, we know that this is not true for all of the genera now restricted to Florida. For example, *Rhineura* is now found solely in peninsular Florida but obviously it has not been completely evolved here since the Miocene, for the genus is known from the Oligocene of Colorado, South Dakota, Nebraska and Wyoming. It seems evident that it, like *Siren,* had a different distribution in earlier times and made its way to the Miocene land mass of Florida. For some reason it has become extinct elsewhere. In Post-Miocene times it has spread but little from that asylum which it found in Florida. The same is true of *Alligator* and *Macroclemmys.* Although the fossil record is lacking, it may be that other reptilian genera, such as *Liodytes,* have had similar histories.

At the present time there is not sufficient basis for any firm conclusions regarding the derivation of *Amphiuma, Abastor, Deirochelys* and *Seminatrix.* In each case the genus involved may have originated on the Miocene land mass of Florida and have subsequently spread, or may be a group that found asylum here during the Miocene and was not wholly eliminated elsewhere, as was for example *Rhineura.*

It seems pertinent to mention one other fact. These genera, whether they originated in Florida through endemism, or whether they simply found asylum here, all have one thing in common—they are secretive forms, either burrowing in mud, like *Pseudo-*

branchus and *Siren,* or in sand, like *Neoseps* and *Rhineura,* or being secretive aquatic creatures, like *Liodytes* and *Macroclemmys.* What there is about Florida that has permitted the evolution and perpetuation of secretive forms is still a matter of conjecture.

Thus we see that the Miocene land mass in Florida, perhaps originally built up as a deltaic plain but certainly an island for much of its history, has served both as a source of evolution for the formation of new genera and also as an asylum for forms that earlier were more wide-spread but that for some reason or other became extinct over much or all of their former ranges.

The fauna that moved into the Miocene land mass of Florida was quite different from that found here at present. None of the six snake genera known from the Florida Miocene is in existence today. Yet in addition to *Siren* a number of modern genera were present, including *Scaphiopus, Bufo, Hyla, Microhyla, Rana, Pseudemys,* and a newt closely allied to, if not actually a member of, the genus *Diemictylus.* Except for the newt and the *Rana,* these are forms with western affinities. They are, for the most part, rather vagile creatures which had wide ranges then and have wide ranges now. They do not seem to have been affected, in an evolutionary sense, to the extent the secretive forms were by the formation and probably later isolation of the Florida Miocene land mass. They got here, it is true, but they were not eliminated elsewhere and apparently they were not sufficiently isolated for a long enough period of time from the mainland populations to give rise to endemic genera. At least, if such genera did originate we have not yet found any fossil record of them and they certainly have not lived up to the present time. It is tempting to hypothesize an archipelago, isolating the secretive burrowers but not forming a complete barrier to 'island-hopping' frogs.

The fact that *Scaphiopus* has been in Florida since the Miocene and the further fact that it is unquestionably a toad of desert affinities gives us some clue to the persistence of breeding habits. In Florida, *Scaphiopus,* living as it has since the Miocene in a land where there are abundant ponds, lakes and streams, still retains its desert habit of breeding in temporary waters only. Furthermore the tadpoles transform at rates indicative of drying puddles. It would seem, then, that the breeding habits of *Scaphiopus* as exhibited in Florida at the present time have remained unchanged at least since Miocene times although it has been away from desert

country where such habits are obligatory for at least that long.

The herpetofauna of the Florida Pliocene was much larger and here we find such modern genera as *Heterodon, Micrurus, Agkistrodon, Crotalus, Ophisaurus* and a *Farancia*-like snake. This Pliocene influx was obviously predominantly western in origin.

In the Pleistocene, many more modern genera made their appearance, including: *Ambystoma, Amphiuma, Plethodon, Acris, Pseudacris, Chelydra, Macroclemmys, Sternotherus, Kinosternon, Trionyx, Gopherus, Anolis, Sceloporus, Cnemidophorus, Storeria, Thamnophis, Diadophis, Rhadinaea* and *Coluber*. Some of these forms, *Kinosternon, Gopherus, Sceloporus, Cnemidophorus, Thamnophis, Diadophis, Rhadinaea* and *Coluber* are western. Any of them may, of course, have reached Florida in the Pliocene, although unrecorded from then as fossils. Many of the Pleistocene genera, such as *Ambystoma, Plethodon, Acris, Pseudacris, Chelydra, Sternotherus, Trionyx* and *Storeria*, were from the eastern United States. This seems to have been the first large influx into Florida from the northeast. By and large the Pleistocene herpetofauna was very similar to that found in Florida today.

Obviously, evolution in Florida did not stop in the Middle Cenozoic. The genus *Sceloporus* has an endemic species in Florida which occupies the habitat known as Rosemary Scrub. In all probability the species *Sceloporus woodi* evolved on Florida Islands, whether Pleistocene or Pliocene, but its differentiation did not take so long as did the evolution of such genera as *Pseudobranchus*. At the present time raciation seems to be occurring in Florida. Many wide-ranging forms have given rise to subspecies on the Peninsula. Some of them may go back to the Pleistocene when much of Florida was undoubtedly insular.

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